Detecting Adaptive Inverse Models in the Central Nervous System

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***Abstract*—This study aimed to find evidence for the formation of an internal inverse model of a novel visuomotor relationship for feedforward control in the brain. An experiment was carried out involving 20 normal adult subjects who performed a pursuit random tracking task with a steering wheel for input. During learning, the response cursor was periodically blanked, removing all feedback about the external system (i.e., about the relationship between hand motion and response cursor motion). Results showed a transfer of learning from the unblanked runs to the blanked runs for a static nonlinear system (linear trend RMS error $F(1,19) = 5.05$, $p = .037$) thereby demonstrating adaptive feedforward control in the nervous system. This result provides the strongest evidence to date that the brain adaptively tunes inverse models of external controlled systems during motor learning. No such transfer was observed for a dynamic linear system, indicating a dominant adaptive feedback control component. Results are consistent with inverse modeling and suggest a combination of feedforward and feedback adaptive control in the brain.**

***Keywords*—Internal model, motor learning, adaptive inverse control, motor control, pursuit tracking.**

I. Introduction

CURRENT theories of human voluntary motor control typically hypothesize that the brain employs adaptive internal models of controlled processes [1-4]. These internal models are used to implement a complex transformation from desired movement trajectory to the corresponding set of efferent motor commands [5, 6]. There are two classes of internal model: forward models and inverse models [7]. Forward models use efference copies of outgoing motor commands to predict the sensory consequences of a movement, while inverse models convert desired sensory consequences into motor commands. Both forward and inverse models capture aspects of the kinematic and dynamic behavior of the environment external to the brain [8].

A motor control system employing an internal model may be categorized as implementing some combination of feedforward and feedback control, depending on the way it utilizes sensory feedback. Feedforward systems typically employ inverse models to effect a desired response, whereas feedback systems often employ forward models to overcome sensorimotor delays [9, 10]. The contribution of each in the human motor control system remains unclear. Adaptive feedback and feedforward control structures usually work in combination in modern motor control hypotheses [11-13] .

The primary aim of this study was to look for evidence of inverse model formation by examining the characteristics of

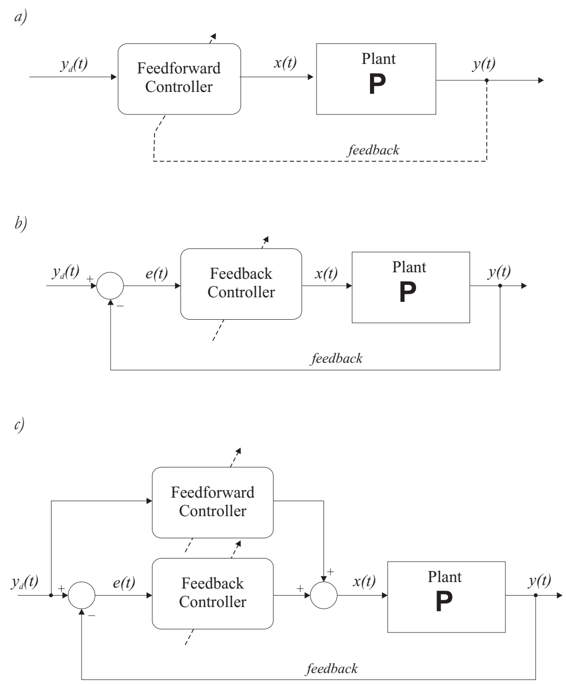

Fig. 1. (a) Adaptive feedforward controller. (b) Adaptive feedback controller (representative structure). (c) Possible parallel combination of adaptive feedback and feedforward control. Dotted arrows indicate adaptation.

feedforward adaptation in the human brain. Beyond this, the study aimed to elucidate the relative extent of the feedforward and feedback control contributions. To achieve this, visual feedback was withheld during learning of a pursuit tracking task. By blanking the response cursor it is possible to completely eliminate feedback of an external tracking system.

Response blanking in a pursuit tracking task offers the opportunity to observe the effect of systematically removing an input signal that is otherwise continuously available. This technique can be used to show adaptive feedforward control in action in the motor system.

When feedback is available, feedforward and feedback adaptive controllers are difficult to distinguish. Both classes of controller use feedback as input for their adaptive processes and consequently exhibit improved performance over time.

In an adaptive feedforward controller, feedback is used to tune an adaptive element such as an inverse model (see Fig. 1a). This model is still available for use when feedback is removed. The action of the controller does not depend on feedback, so withholding it simply suspends the adaptation. Performance otherwise remains unaffected. During normal

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Abstract

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operation, the model is tuned and controller performance gradually improves. A similar gradual improvement should therefore be evident in the feedback-free performance of the controller when deprived of feedback periodically during learning.

Assuming adaptation is temporarily halted when feedback is removed, a plot of temporal variation in performance with feedback (unblanked performance), and corresponding performance without feedback (blanked performance), can then be constructed. If all the unblanked learning is indeed captured in an inverse model (as predicted for ideal adaptive inverse control) then a direct proportional improvement in blanked performance will be evident (Fig. 2a).

An adaptive feedback controller (Fig. 1b) will also gradually improve its performance when feedback is available. When feedback is removed, however, an inappropriate control effort is produced because a feedback controller depends on a continuously available feedback signal. In a plot comparing ideal unblanked and blanked performance a feedback controller shows no performance improvement when blanked (Fig. 2b).

If both feedforward and feedback adaptive elements are present in the controller (Fig. 1c), the results would show some (unequal) improvement in blanked performance (Fig. 2c). Fig. 1c shows a parallel combination of adaptive elements but a series combination is also possible and does not alter the interpretation of results. Assuming all blanked improvement is due to the action of an adaptive feedforward component, the relative contribution of each control component can be estimated. Note that it is also possible for a combination controller to exhibit no improvement in unblanked performance while showing strong improvement in blanked performance, since the feedforward component can learn from superior feedback behavior [12].

Feedback blanking, therefore, gives us a method both for detecting adaptive feedforward control in the motor control system and for judging the extent of the contribution of each mode of control.

II. Methodology

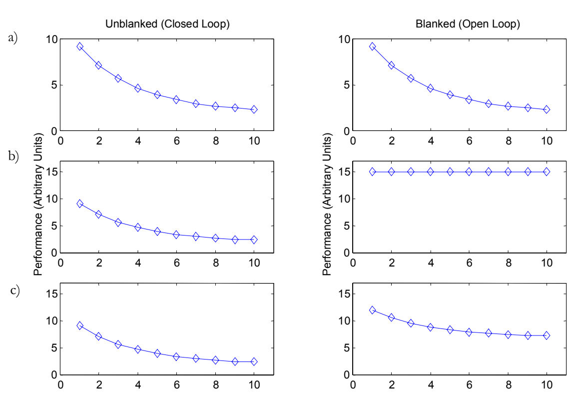

Fig. 2. Tracking performance for ideal adaptive (a) feedforward, (b) feedback and (c) combined controllers. The blanked runs are performed immediately

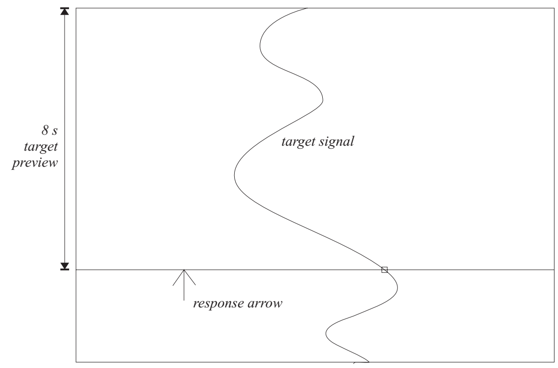

Fig. 3. Tracking task display screen.

Subjects were trained on a pursuit tracking task with visual feedback for a short interval, during which they partially learned to control the system. Feedback was then removed by blanking the response cursor. This training and blanking cycle was repeated several times until no further unblanked learning was evident.

The performance of the subjects in each interval was then assessed. Improvement in blanked performance was interpreted as adaptive feedforward learning and, therefore, as evidence for the formation of an adaptive inverse model.

A. Subjects

Twenty subjects (13 male and 7 female) with no history of significant neurological or musculoskeletal disorder participated in the study. All subjects passed a standard visual acuity test prior to beginning the experiment, which confirmed their ability to resolve 1 pixel (0.31 mm at 130 cm) on the screen. The ages of the subjects ranged between 20 and 56 years (median 29.5 years) and the group included 3 left-handed individuals. The subjects were randomly divided into two equal sub-groups labeled ‘A’ and ‘B’, each of which learned to control a different system.

B. Apparatus

The apparatus included a PC with two color monitors: one displaying test stimuli for the subject and the other used by the assessor for task generation and analysis. All tests were run and analyzed with the program SMTests [14]. Subjects were seated in front of their monitor (312 x 234 mm) with an eye-to-screen distance of approximately 130 cm. All of the visuomotor tests were one-dimensional and employed a steering wheel (395 mm diameter) as the subjects' output sensor. Rotation of the wheel moved an arrow horizontally on the screen (see Fig. 3).

Both the screen response and the motor output response were recorded for analysis. Data was sampled at 60 Hz — the screen update rate — which is well above the Nyquist sampling frequency.

C. External Systems

Group A controlled a linear dynamic external system. The dynamics were produced by passing the motor response

through an IIR filter: a 3rd order Chebyshev Type I low-pass filter with cutoff frequency of 3 Hz.

Group B was required to learn a static nonlinear system. The system was a cubic function of input angle, scaled to provide a challenging variation in gain while remaining controllable. The function was displaced from center to increase the difficulty of the task by avoiding symmetry.

D. Target

The target signal comprised two consecutive sections as follows:

1) Unblanked Training Signal: 68 s of a pseudo-random waveform generated from superposition of 50 sinusoids of equal amplitude and equally spaced in frequency with random phase from 0.007 Hz up to 0.6 Hz, 75% full scale deflection. The random nature of the signal ensured that the dynamic controlled systems were excited sufficiently to allow the subject to maximally learn their characteristics.

2) Blanked Assessment Signal: Identical to the first 28 s of the training signal except for removal of feedback to the subject by turning off the response arrow.

The two sections were combined and separated by a 7-s interval where the target returned to the center of the screen. All three sections combined to form a single continuous 103-s target signal, which was used for all runs in the experiment. The subject was also presented with an 8-s preview of the target to eliminate the need to predict the target signal and, hence, minimize a possible confounding source of learning.

III. Experimental Procedure

The experiment comprised 25 consecutive tracking runs, each of 103-s duration (i.e., the length of the target signal). For each run the following procedure was followed:

1. The investigator positioned the screen pointer exactly on top of the target thereby preventing the subject from gaining knowledge of the system prior to the run.
2. The subject was asked to hold the wheel at the marked position (top-center) with their dominant hand.
3. The subject was asked to ‘keep the point of the arrow on the line as accurately as possible’.
4. The subject was told that the arrow would disappear late in the run and that they were required to continue the task by estimating the position of the arrow.
5. When the subject was ready, the investigator started the run.
6. On completing the run, the subject was told their mean absolute error (MAE) score for the unblanked section of the run (as an incentive to improve their performance).
7. The subject was then given a minimum 20-s rest (to prevent fatigue) before commencing the next run. A 5-min rest was given following the 10th run.

The total time for a complete session averaged 70 min.

All subjects were initially asked to control a simple zero-order external system (i.e., wheel angle proportional to response pointer position). These practice sessions were intended to allow the subjects to learn as much about the target and tracking system as possible. This facilitates the assumption made later in analysis that only the external system was learned in the following runs.

Ten runs of the zero-order task were performed, after which learning was deemed to have essentially plateaued. At this point the stochastic characteristics of the target signal, the kinematic and dynamic properties of the steering wheel, and the wheel-to-display relationship are considered to have been maximally learned.

The subjects were then asked to control a new visuomotor relationship, implemented by altering the characteristics of the external system. The specific external system they were to control depended on which group they belonged to.

Both groups were required to train on their new external system for 15 runs. This duration was selected to be long enough to characterize any learning trend but not so long as to introduce noticeable fatigue.

IV. Results

A. RMS Error

The linear trend analysis of RMS-error results are summarized in Table I. A significant linear trend of reduction in RMS error was observed in both the unblanked and blanked practice runs ($p < .001$). The unblanked and blanked runs showed unequal reduction in mean RMS error from the first run to last run (33% improvement unblanked vs. 18% improvement blanked).

The unblanked practice runs showed no significant linear trend over runs 6 to 10 ($F(1, 19) = 1.40$, $p = .25$), suggesting that the learning effect was confined to the first half of the practice runs and supporting the assumption that learning had essentially plateaued by the end of practice. Similarly, no linear trend was observed over runs 6 to 10 for the blanked runs ($F(1,19) = 3.26$, $p = .087$).

Group A showed the strongest learning in the unblanked section (54% reduction in mean RMS error) but, surprisingly, exhibited no discernible learning trend in the blanked section.

Group B showed substantial improvement in the unblanked section, although to a lesser degree than that observed for Group A (Fig. 4). However, in contrast to Group A, performance was seen to improve with a significant linear trend during the blanked sessions ($p = .037$, see Table I). Group B did not show a proportional reduction in mean RMS error from the first run to last run in the blanked and unblanked responses (35% improvement unblanked vs 17% improvement blanked). This difference suggests a feedback control component for Group B.

Table I. Linear Trend Analysis for RMS Error

Group	**Unblanked Runns** *(log transform)*							**Blanked Runs**					
	Effect		*Error*					*Effect*		*Error*			
	df	*MS*	*df*	*MS*	*F*	*p*		*df*	*MS*	*df*	*MS*	*F*	*p*
Practice	1	0.762	19	0.006	137.3	0.000	***	1	14.16	19	0.679	20.8	0.00
A	1	0.923	18	0.004	239.6	0.000	***	1	23.6	18	767.8	0.0	0.86
B	1	0.246	18	0.004	64.0	0.000	***	1	3879	18	767.9	5.1	0.03

$p < .05$ = *, $p < 0.01$ = **, $p < 0.001$ = ***, A = Dynamic Linear, B = Static Nonlinear

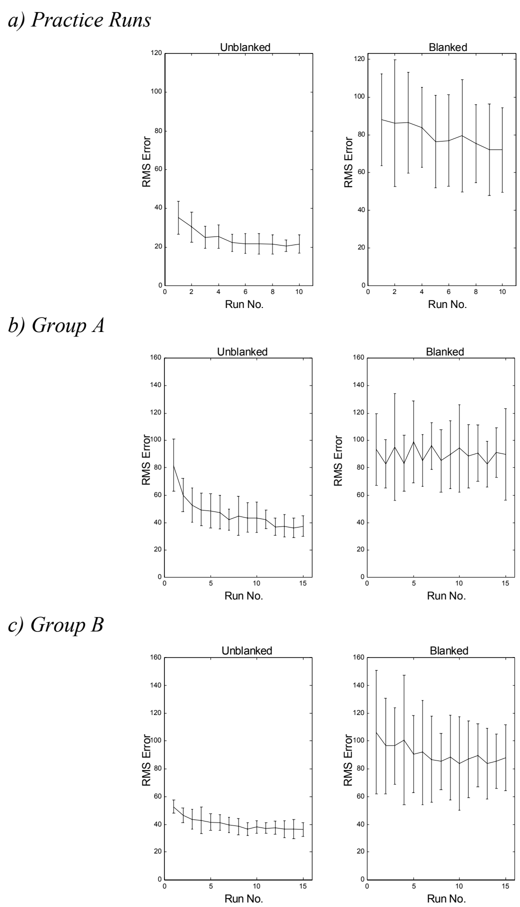

Fig. 4. Mean RMS error scores. Error bars show standard deviation.

B. *Spectral Analysis*

An error spectral analysis was carried out to confirm that the RMS error results were not biased by low frequency drift. The analysis confirmed all important RMS error results. For the blanked runs Group A showed no significant learning trend at any frequency while Group B showed learning from 0–0.3 Hz, $p < .05$.

V. Discussion

The finding of a reduction in RMS error over the blanked runs for Group B is consistent with adaptive feedforward control of a static nonlinear external system. Analysis of the error spectra confirmed this result, with learning trends in the lower half of the target bandwidth. This result provides the strongest evidence to date that the brain adaptively tunes inverse models of external controlled systems during motor learning. Conversely, the data did not reveal the simple learning transfer from unblanked to blanked runs that would be expected for a pure adaptive inverse controller, hence suggesting the presence of an adaptive feedback control contribution.

No blanked performance improvement was observed for the dynamic linear external system, in RMS error or in the error spectral analysis, despite strong improvement in both during the unblanked runs. This indicates the importance of adaptive feedback in the control of difficult dynamic external systems.

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